

American Museum Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK 24, N.Y.

NUMBER 2068

DECEMBER 29, 1961

Notes on Flowerpeckers (Aves, Dicaeidae) 6. The Superspecies *Pardalotus striatus*¹

BY FINN SALOMONSEN²

The present paper, which concludes the "Notes on flowerpeckers,"³ deals with the taxonomic units that are usually designated as *Pardalotus striatus* (= *affinis*), *ornatus* (= *assimilis*), *substriatus* (formerly incorrectly called *ornatus*), *melanocephalus*, and *uropygialis*. They form an assemblage of very closely allied forms and can be united into a superspecies. From a zoogeographic, an evolutionary, and a taxonomic point of view, this group poses most interesting and intriguing problems, which necessarily require comments of some length.

The superspecies constitutes a chain of incipient species connected by zones of secondary intergradation. One of the hybrid populations has been developed into a separate species (*ornatus*). This species interbreeds with *substriatus*, and *substriatus* interbreeds with *melanocephalus*, but this last-named is unable to interbreed with *ornatus*. Such a situation is quite extraordinary.

Another interesting group is the chain *substriatus-melanocephalus-uropygialis*. The members of this chain produce hybrid zones where they come in contact, but where the two end links (*substriatus* and *uropygialis*) meet they behave as two allopatric species and may even, in a re-

¹ The costs of publishing the present paper were paid from the Frank M. Chapman Memorial Fund.

² Curator of Birds, Zoological Museum, Copenhagen, Denmark.

³ The earlier papers in this subseries are American Museum Novitates, nos. 1990 (1960), 1991 (1960), 2016 (1960), 2057 (1961), and 2067 (1961).

stricted area, live side by side, but such a possibility has not been demonstrated with certainty.

It is difficult taxonomically to treat such groups, in which two forms are connected by a continuous chain of populations but mutually are reproductively isolated and behave as two good species. They form borderline cases between species and subspecies and are of considerable interest in the study of evolution. Similar borderline cases are known in other groups of birds, such as *Larus argentatus-fuscus* and *Phylloscopus trochiloides-plumbeitarsus*, summarized by Mayr (1942, Systematics and the origin of species, pp. 180–185), or, to quote an Australian example, *Platycercus elegans-flaveolus* (cf. Cain, 1955, Ibis, vol. 97, pp. 456–461). The case of *Dicaeum agile-everetti* could also be mentioned (cf. Salomonson, 1960, Amer. Mus. Novitates, no. 1991, p. 5, fig. 1).

In the case of the pardalotes the one extreme view is to lump them all, recognizing only one species, while the other extreme is to regard them as five separate species. I find the acceptance of four species the most satisfactory arrangement, but I do not attach much weight to the actual number of species in which this group is split. In complicated cases such as this the ordinary system breaks down, and the arrangement must always be arbitrary. The main thing is that these pardalotes stand on the verge between subspecies and species and represent different stages in the process of speciation.

The so-called striated pardalotes comprise three taxa, which constitute monotypic sibling species (*striatus*, *ornatus*, and *substriatus*) and are characterized by having the upper parts of the head black, with distinct, white, longitudinal streaks. The group of the black-headed pardalotes consists of two taxa (*melanocephalus* and *uropygialis*), which here are regarded as conspecific. They differ from the striated pardalotes in having the upper parts of the head uniform black. Apart from this difference *P. substriatus* and the nominate form of *P. melanocephalus* are amazingly alike. There is, in addition, a noteworthy difference in nest building between the striated and the black-headed pardalotes, which further justifies the separation of the latter as a full species, in spite of the similarity to, and the hybridization with, *substriatus*. All populations of *P. melanocephalus* invariably build their nests in burrows excavated in the soil or in banks, while the three species of striated pardalotes usually build in tree holes, although many instances are known of their ability to tunnel the nest in banks.

The distribution of the units belonging to the superspecies *P. striatus* and the situation of the hybrid zones are outlined in figure 1. The genetic nature, or rather the phenotypic composition, is different in

each of the three hybrid populations.

The hybrid zone between *melanocephalus* and *uropygialis* is extensive and broad. The hybrids display every possible color gradation between the two parental forms and exhibit a similar variation in body proportions. In localities within the hybrid zone situated near the area inhabited by pure *melanocephalus*, the characters proper to this form dominate the phenotype of the hybrids, some individuals even being indistinguishable from *melanocephalus*. As one moves through the zone of interbreeding, populations with continuously changing compositions are encountered, with a gradually increasing admixture of *uropygialis* characters, until these predominate at the border of the range of *uropygialis*. Probably no two populations are similar, and in the central parts of the hybrid zone both parental forms are lacking, which tends to show that a large number of genetic factors are involved in producing the special phenotype of the hybrids. The considerable extent of the zone of interbreeding, and the high frequency of the hybrids compared with that of the parental forms, make it natural to consider this hybridization as an infraspecific phenomenon and, consequently, to regard the two parental forms as conspecific.

Formerly *uropygialis* and *melanocephalus* were considered two separate species, but modern students invariably regard them as ordinary subspecies of a single species. Apparently, no one has realized that the two forms are connected by an extensive zone of secondary intergradation.

The hybrid zone between *melanocephalus* (the nominate subspecies) and *substriatus* is a rather narrow belt. The two parental forms differ from each other in five separate characters, one being size, and in the hybrids these five characters vary independently of one another and are freely combined. Individuals with a phenotype similar to the two pure forms evidently occur throughout the zone of interbreeding but are greatly outnumbered by the hybrids, at least in those localities from which I have examined material. The hybridization between these two species has hitherto escaped the notice of students.

It is a matter of opinion whether *melanocephalus* and *substriatus* are treated as conspecific or regarded as two separate species. We have at present only a superficial knowledge about the hybrid zone between *melanocephalus* and *substriatus*, and for the time being I find it most convenient to separate these two forms specifically. Even ecological factors (differences in nest building) speak in favor of this view, as mentioned above. Nothing is known about the way in which the hybrids build their nests. Another factor that in my opinion makes it inadvisable to regard *melanocephalus* and *substriatus* as conspecific is the lack of inter-

breeding between *substriatus* and *uropygialis* where these two forms come into contact.

Possibly *melanocephalus* and *substriatus* do not interbreed everywhere in the zone of range overlap. Lord (1956, Emu, vol. 56, p. 122), who handled a number of breeding pardalotes in the Murphy's Creek district, southern Queensland (between Brisbane and Toowoomba), found *substriatus* commonly, and *melanocephalus* sparingly, breeding, but apparently without interbreeding.

The hybrid zone between *melanocephalus* and *substriatus* partly overlaps that between *substriatus* and *striatus* (cf. fig. 1), and consequently triple hybrids could be expected to occur in this zone. Evidently, such is not the case. All hybrids examined are either typical *substriatus* \times *striatus* (i.e., *ornatus*) or distinct *melanocephalus* \times *substriatus* which exhibit no signs whatever of influence from *striatus* or *ornatus*, a fact that points strongly to the conclusion that *melanocephalus* is unable to hybridize with *striatus* as well as with *ornatus*.

The complicated relationship between the three forms of striated pardalotes (*striatus*, *ornatus*, and *substriatus*), which live sympatrically in an extensive area of southeastern Australia, has been much discussed by Australian zoologists. These birds have been looked upon very differently and have been considered as forming either a single species (e.g., by Mathews, 1923, The birds of Australia, vol. 11, pt. 3, p. 195), two species (e.g., by the Royal Australasian Ornithologists' Union, 1926, The official checklist of the birds of Australia, ed. 2, p. 92), or three species (e.g., by Hindwood and Mayr, 1946, Emu, vol. 46, p. 49).

The main thing is that in the zone of overlap between the range of *substriatus* and that of *striatus* the population is composed of an exactly intermediate and remarkably constant form (*ornatus*), as well as pure *striatus* and *substriatus*. The differences between the three forms are few and clear-cut, namely: wing patch, formed by the tips of the primary coverts, yellow in *striatus*, red or orange-red in *ornatus* and *substriatus*; edge of outer web white on the third primary in *striatus* and *ornatus* (frequently also on the fourth primary in *ornatus*), and on the third to eighth (occasionally to the seventh or to the ninth) in *substriatus*. In addition, there is a difference in size. The two forms *ornatus* and *substriatus* are exactly similar in proportions—wing length, bill, and tarsus—while *striatus* is decidedly a larger bird. From table 1 it appears that 58 specimens of *ornatus* have a wing length of 62–67 (average 64.9) mm., and 20 specimens of *substriatus* from the same states (Victoria and New South Wales) a wing length of 63–67 (average 64.7) mm. This shows a virtual identity of the two forms. The wing length of 11 specimens of

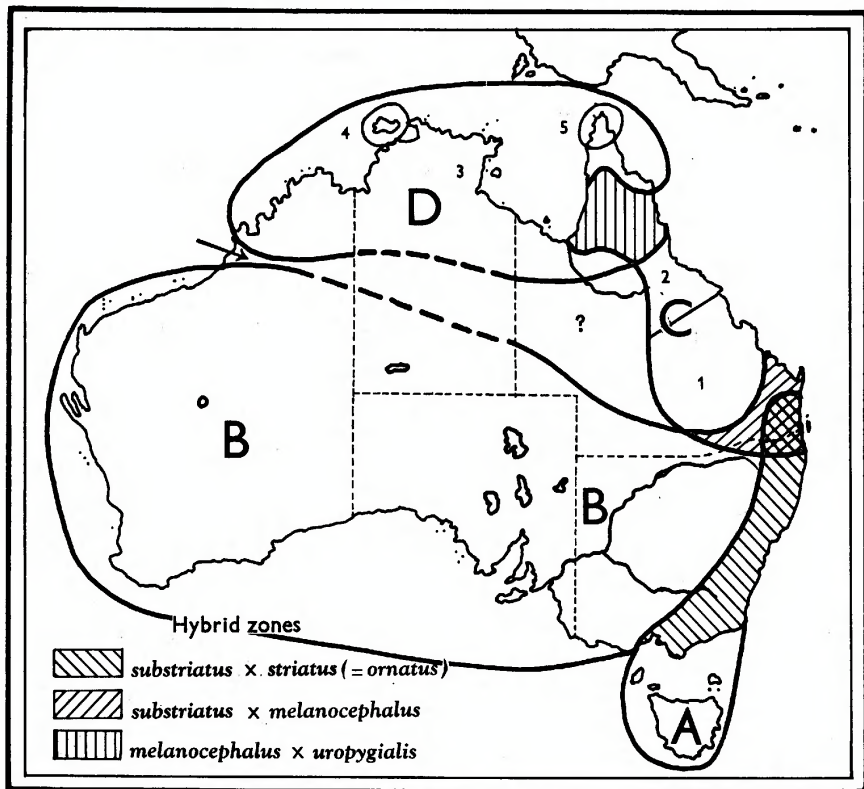


FIG. 1. Range of the superspecies *Pardalotus striatus*, indicating the hybrid zones between the species. A. *striatus*. B. *substriatus*. C. *melanocephalus*. D. *uropygialis*. The arrow points at the narrow gap between the range of *substriatus* and that of *uropygialis*. The numerals mark the ranges of the subspecies within the *melanocephalus*-*uropygialis* group (1, *melanocephalus*; 2, *bowensis*; 3, *uropygialis*; 4, *melwillensis*; 5, *restrictus*).

striatus from Victoria and New South Wales is 66–68 (average 66.9) mm. There is a similar difference in the wing/tail ratio between *striatus* and the two other forms, as pointed out by Hindwood and Mayr (*ibid.*, p. 60). In *striatus* the tail constitutes on an average 53.2 per cent of the wing length, while in *substriatus* the corresponding figure is 51.6 and in *ornatus* 51.3.

While Hindwood and Mayr (*loc. cit.*) held all three forms to be separate species, such a hypothesis was opposed by Serventy (1953, *Emu*, vol. 53, p. 136), who strongly advocated the view that the three forms constitute one species, *ornatus* being a hybrid between *striatus* and *substriatus*. My conclusion may appear rather ambiguous, because I think

that both viewpoints are correct. I must admit, however, that the status of *ornatus* is still not entirely clarified. Much work, especially field work, is needed to solve the problem of the real nature of *ornatus*.

The following facts speak in favor of the hybrid status of *ornatus*:

1. It is an exact intermediate between *striatus* and *substriatus*.
2. It is restricted precisely to that area in which the ranges of *striatus* and *substriatus* overlap.
3. Although remarkably constant in its morphological characters, *ornatus* is, nevertheless, slightly more variable than the two other forms, particularly in the extent of the striation on the head, the forehead being sometimes pure black, and in the forms of the streaks. This relative instability of *ornatus*, which has been emphasized also by Hindwood and Mayr (*ibid.*, p. 55), indicates hybrid origin, although the individual variation admittedly is much less than would be expected in a hybrid population.
4. Intergrades between *ornatus* and one of the two other forms are known, although they are very rare.
5. Mating between *substriatus* and *ornatus* has been observed with certainty, though only a few times. The most recent observation was made by Lord (1956, *Emu*, vol. 56, p. 122), who states that "Several times I have found *substriatus* and *ornatus* mated. Birds handled at the nest show one with two white-lined primaries and the other with six to seven tipped with white."¹
6. The three forms in question (*striatus*, *ornatus*, and *substriatus*) display no habitat segregation or other biological differences. It is especially noteworthy that they have a similar form of nest building, differing from that of all other species of pardalotes (a domed nest placed in a tree hole).

This evidence appears to be overwhelmingly in favor of the hybrid hypothesis, and I cannot see that the available facts permit any other explanation of the peculiar coexistence of the three forms in south-eastern Australia.

The above argument is, however, not the whole truth about the status of *ornatus*. A closer study of the situation in the zone of interbreeding reveals certain discrepancies which cannot be explained by the hybrid hypothesis. The first point concerns the constancy of *ornatus*, which is a quite extraordinary phenomenon in hybrid populations, in which normally a pronounced segregation of characters takes place.

¹ After the present paper was finished, Cooper (1961, *Emu*, vol. 61, p. 1) published new instances of matings between *substriatus* and *ornatus*.

Even more peculiar is the fact that in the zone of interbreeding the hybrid form vastly outnumbers the two parental forms, both of which are extremely rare. This has been expressly emphasized by Hindwood and Mayr (*loc. cit.*) and, further, is apparent from a study of the museum collections. Evidently, *striatus* and *substriatus* are on the way to being wiped out in the zone of interbreeding, which tends to show that the hybrid must have a considerable selective advantage in this area, probably in connection with viability. The relation between the three forms resembles mostly a system of balanced polymorphism. It is obvious that the hybrid population now is entirely independent of the two parental forms. The extremely low influx of genes emanating from the very few individuals belonging to the two parental forms must be virtually without effect on the gene pool of the hybrid population. The morphological uniformity and constancy of the latter indicate that the hybrid characters have been stabilized and that the original hybrid has reached species level or at least must be regarded as an incipient species. This view is strengthened by the fact that only very few instances of mating between different forms have been recorded, in spite of the fact that the hybrid zone is situated in ornithologically well-worked parts of southeastern Australia, where striated pardalotes are common forest and park birds. This indicates selective mating, or it may be explained by the scarcity of the two parental forms in the area of interbreeding.

It is noteworthy that the body proportions of *ornatus* are similar to those of *substriatus* and are not in an intermediate position between those of the two parental forms, such as is the case in the hybrids between *uropygialis* and *melanocephalus* and in those between *substriatus* and *melanocephalus*. This does not by any means weaken the hypothesis concerning the hybrid nature of *ornatus* but simply indicates that the size variation is dependent on only a few Mendelian factors (or a single one) and that the genotype of *substriatus* is dominant in this respect. The color marks of *ornatus* are transmitted similarly; the *substriatus* gene is dominant as regards wing patch color, while the *striatus* gene is dominant as regards the extension of white in the primaries.

It is possible to obtain a clearer but very schematical and undoubtedly much too simplified picture of the situation by using symbols, calling the gene for wing patch *A*, that for white on primaries *B*, and that for size *C*. The genetic formula of *striatus* is then *aaBBcc*, that of *substriatus* *AAbbCC*, and that of the first generation of hybrids *AaBbCc*. The recombinations in the subsequent generations will naturally give rise to considerable segregation, but the different gene combinations cannot possibly have the same survival value. Some of them must have

deleterious effects or must, at least, cause a lowered viability, or the phenotypic picture of the *ornatus* population would be much more varied and complicated. The majority of the present population of *ornatus* one may assume has reached the homozygotic stage *AABBCC*, which would insure heredity against noxious segregation,¹ especially when furthered by selective mating. At any rate, it would explain the remarkable constancy of the hybrid, but at the same time it would imply that *ornatus* had almost attained specific status. This possibility has been stressed also by Hindwood and Mayr (*ibid.*, p. 65), who state that "it might be suggested that the species *ornatus* owes its origin to a hybrid population between *striatus* and *substriatus*, developing in a wide zone of overlap of these two species. Such a hypothesis faces many difficulties, the greatest of which is the necessity to explain how sexual isolation could have developed between the former 'hybrid population' *ornatus* and the two parental populations when they themselves freely interbreed."

Against these considerations is the objection that whether or not the two parental populations have ever "freely interbred" is unknown. Presently, not a single case is known of mating between *striatus* and *substriatus*. Hybridization may have taken place only occasionally but may eventually have resulted in the firm establishment of a hybrid with a genotype which for some reason (homozygosity?) was superior to all other gene combinations.

This form of speciation, taking place through the establishment of a stabilized hybrid population, is an extremely rare phenomenon in birds.² Nevertheless, one certain point tends to show that the specific separation of *ornatus* actually is the result of such speciation. Granted that the genotype of *ornatus* has superior selective value in the area of coexistence with *striatus* and *substriatus*, and that selective mating takes place to a very high degree, intergrades between *ornatus* and either of the parental forms would be very scarce, partly because such individuals would be

¹ This view is not in conflict with the general assumption of geneticists that homozygosity is inferior to heterozygosity, in so far as increased heterozygosity adds to fitness, providing for greater plasticity. The development of *ornatus* may have taken place by means of introgression (cf. Anderson and Stebbins, 1954, *Evolution*, vol. 8, pp. 378-379), but a further discussion of this subject falls outside the scope of the present paper.

² Other supposed cases of this form of speciation in birds have been enumerated by Ripley (1958, *Postilla*, no. 35, p. 5), Gilliard (1959, *Amer. Mus. Novitates*, no. 1937, p. 20), and Salomonsen (1951, *The birds of Greenland*, pp. 515-516), concerning species within the genera *Anas*, *Junco*, *Pipilo*, *Passer*, *Carduelis*, *Melidectes*, *Pycnonotus*, and others.

inferior in genotype to the three "pure" (i.e., homozygotic) forms, and partly because interspecific crossings would be rare. The situation would be different in the outskirts of the area of coexistence, where the population of *ornatus* is thin, or outside this area, where *ornatus* (and *striatus*) normally do not occur but where *substriatus* is a common bird. In such localities the acceptance of an individual belonging to *substriatus* may become the only mating chance for a stray *ornatus*, and at the same time the offspring will probably be less inferior in viability owing to lessened competition. Consequently, such intergrades would be expected to occur much more frequently in such areas than in regions with a dense population of *ornatus*. Actually, such appears to be the case. Hindwood and Mayr (*ibid.*, p. 60) mention six specimens which are intermediate between *ornatus* and *substriatus* and which they consider hybrids between these two species. These specimens have white outer webs on the third, fourth, and fifth (one specimen even on the sixth) primaries. One of these specimens is without locality, and one is from Sydney. The four remaining ones are from the border range (or outside the normal range) of *ornatus*, namely: one from Chinchilla, situated rather far north in southeastern Queensland; one from Dubbo, slightly west of the normal range of *ornatus* in New South Wales; one from Castlemaine, Victoria, which is in the border zone of the range of *ornatus* in this state; and one from Mildura in Victoria, far off the normal range of *ornatus*.¹ Thus four out of five (six?) intergrades originate from localities situated in the border zone of the range of *ornatus*, while only one (two?) has been obtained in the central parts of the range, where collecting has been much more intense, a fact that strongly supports the hypothesis set forth above.

In this connection it is noteworthy that the locality (southeastern Queensland) in which Lord (*loc. cit.*) found regular matings between *ornatus* and *substriatus* is situated in the border zone of the range of *ornatus*. Lord expressly states that *substriatus* is common and *ornatus* "fewer in number." The localities (north of the Dividing Range in Victoria) from which Cooper (1961, *Emu*, vol. 61, p. 2) recently recorded matings between the two species are, likewise, situated in the border zone of the range of *ornatus*.

Hybrids between *ornatus* and *striatus* are virtually unknown, a fact that fits well with the considerations above. Only two specimens with a phenotype intermediate between that of *striatus* and that of *ornatus* are

¹ This last specimen is mentioned by Hindwood and Mayr (*ibid.*, p. 58) but strangely enough is not considered a hybrid by them.

known, according to Hindwood and Mayr (*loc. cit.*), one without locality, the other from Western Australia, the latter obviously being a rare aberration and not a hybrid. As mentioned above, not a single case is known of mating between *striatus* and *substriatus*.

On the basis of the above considerations it is possible to draw the following conclusions: The hybrid (*ornatus*) has achieved specific status, but still occasionally interbreeds with one of the parental forms (*substriatus*) in the border zone of its range, where only *substriatus* (and not *striatus*) occurs, while in the central parts of its range it virtually never interbreeds with any of the two parental forms. The two latter forms have now apparently ceased to interbreed. Consequently, the three forms must be regarded as full species, a view that is in agreement with that held by Hindwood and Mayr (*loc. cit.*).

There are other alternatives to explain the status of *ornatus*. Hindwood and Mayr favor the hypothesis that *ornatus* originally formed a southeastern Australian subspecies, the range of which was invaded by *substriatus* from the west as well as by *striatus* from Tasmania. This hypothesis is discussed further below.

Another alternative is that *ornatus* forms a color phase of *substriatus*, with which it agrees in all characters except one (the extension of white on the primaries) and with which it occasionally intergrades. However, this hypothesis leaves unexplained a number of facts, of which the most important is that the alleged *ornatus* phase occupies precisely the same area as the alien species *striatus*, at the same time being almost exactly intermediate between the *substriatus* phase and the species *striatus*. It is also improbable that the only two changes in wing pattern in the entire superspecies (in the phase *ornatus* and in the species *striatus*) should be exactly similar, if they had taken place in two different species, independently of each other. It would, further, be peculiar if the *substriatus* phase freely interbred with *melanocephalus*, while the *ornatus* phase was unable to do so. Another peculiarity is the selective mating, which breaks down in the outer range of the *ornatus* phase, and there are also other discrepancies.

It is more difficult to dismiss the hypothesis that all forms (*striatus*, *ornatus*, and *substriatus*) belong to one single polymorphic species. In other birds there are polymorphic populations with a genetic composition and a distributional pattern apparently not unlike that in the striated pardalotes. The flycatcher genus *Terpsiphone*, which comprises many strongly polymorphic species, displays a number of such examples. Populations inhabiting humid forests may consist of three or four variants, differing in both color pattern and body proportions, while only

one variant is left in the populations of the neighboring arid areas and in those of adjacent islands. This situation strikingly resembles that in the striated pardalotes. The parallelism is, however, not complete. The fact that only *substriatus*, and not *striatus* or *ornatus*, is able to hybridize with *melanocephalus* is inconsistent with the view that all three striated pardalotes should form part of one polymorphic species. Also the selective mating, mentioned above, argues against this hypothesis.

The history of the superspecies *Pardalotus striatus* requires the former existence of four isolates. It is noteworthy that these evidently originated in areas in which the development of major faunal elements in Australia took place. The originally undifferentiated population of the present superspecies obviously inhabited the two peripheral zoogeographic subregions, namely, the northern coastal (Torresian) area and the eastern coastal (Bassian) one. The isolation of these two regions accounts for the separation of the northern, Torresian species, *melanocephalus*, from the southern, Bassian one, *substriatus*, of which the former is still restricted to its original range. Both subregions, at a later date, were divided into two isolated areas: the Bassian subregion owing to the insular nature of Tasmania, the Torresian subregion by extreme aridity which developed in the area at the head of the Gulf of Carpentaria. The formation of these barriers gave rise to the isolation between the present *striatus* and *substriatus*, and between *melanocephalus* and *uropygialis*, respectively.

This quadripartition precisely corresponds to the zoogeographic concept of Iredale (cf. Keast, 1959, Monogr. Biol., vol. 8, p. 130, fig. 3), his four subregions denoting the original range of *uropygialis* (1b), *melanocephalus* (1a), *substriatus* (2a) and *striatus* (2b), respectively. Even Campbell's system (cf. Keast, *loc. cit.*) matches the distribution pattern of these pardalotes, his five provinces indicating the former range of *uropygialis* (1), *melanocephalus* (3), *substriatus* (4), and *striatus* (5), while the present zone of hybridization between *uropygialis* and *melanocephalus* (2) was uninhabited.

The probable original ranges of the four components of the superspecies have been mapped in figure 2 in the present paper.

The immature birds of all the forms belonging to the superspecies have the upper parts of the head uniform brownish and unstreaked. It is obvious, therefore, that *melanocephalus* is nearest the common ancestor. The development of the striated head took place in the Bassian population after the separation from the Torresian one. The two neighboring forms, the Torresian *melanocephalus* and the Bassian *substriatus*, are still very similar and differ from each other mainly in the presence

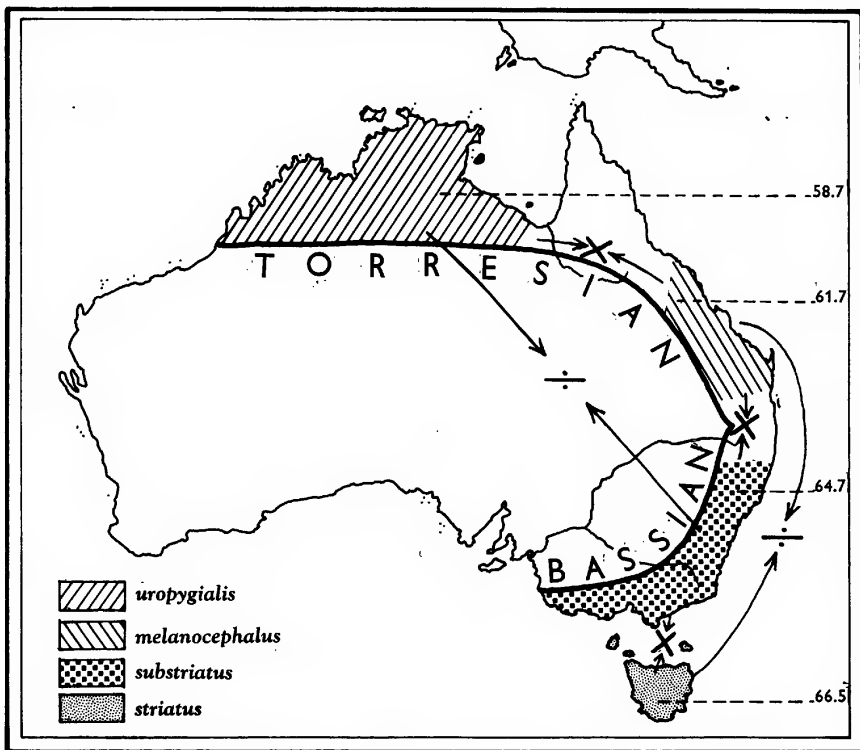


FIG. 2. The alleged original distribution of the elements belonging to the super-species *Pardalotus striatus*. The numerals to the right give the average wing length (in millimeters) of the present populations. Arrows pointing at a cross indicate species that form present hybrid zones; arrows pointing at a minus sign indicate species that are unable to hybridize.

or absence of the striation on the head. The two distant forms (*uropygialis* and *striatus*), on the other hand, have diverged considerably.

Pardalotus uropygialis bears all the earmarks of having developed in an arid and hot climate. It is smaller and paler than *melanocephalus* and has exchanged the chestnut color of the latter with yellow.

In the Tasmanian population, the present *striatus*, the wing pattern, which is uniform in the three other original forms, was altered and adopted a more generalized appearance (reduction of white on primaries, change of red wing patch into yellow), probably as a result of the island conditions.

The average wing lengths of the four populations are shown in figure 2. There is a pronounced increase in size from north to south, which

is in accordance with Bergmann's rule and indicates that the climatic conditions prevailing in the ranges of the four isolated populations differed considerably, which fits well into the hypothesis that is set forth here, because the four hypothesized isolates must have been subject to environmental temperatures which became gradually lower from north to south.

When the geographic barriers between the isolated units broke down, the three continental neighboring forms came into contact, which resulted everywhere in the development of hybrid zones. *Pardalotus uropygialis* moved eastward, occupied Cape York Peninsula, and hybridized with *melanocephalus* in a broad zone at the base of Cape York Peninsula (Normanton-Cairns). This hybrid zone eventually extended westward to the Gulf of Carpentaria, separating the main population of *uropygialis* from that in the northern part of Cape York Peninsula (cf. fig. 1). From a genetic point of view this latter is now probably as effectively separated from the main population of *uropygialis* as if it were isolated on an island.

A similar hybrid zone, extending from Normanton to Cairns, has recently been described in the superspecies *Poëphila cincta* (Keast, 1958, Emu, vol. 58, p. 233). While nominate *cincta* is the counterpart of *Pardalotus melanocephalus*, the other parental form (*atropygialis*) was isolated in Cape York Peninsula, an area that, in the case of the pardalotes, probably was unoccupied in the period of isolation. The counterpart of *Pardalotus uropygialis*, isolated west of the Gulf of Carpentaria, developed into a separate species, the present *Poëphila acuticauda*.

To the south, *Pardalotus melanocephalus* came into contact with the Bassian *substriatus*, which resulted in the formation of another hybrid zone. This zone is narrower than that formed by the interbreeding of *melanocephalus* and *uropygialis* and is not complete, in so far as the two species apparently sometimes live side by side without interbreeding. The differences between the two zones of hybridization tend to show that *substriatus* has drifted farther apart from *melanocephalus* than has *uropygialis*, which is undoubtedly somehow connected with the fact that *substriatus* has been separated from *melanocephalus* for a longer period of time than has *uropygialis*.

Subsequent to the lifting of the barriers that separated the Bassian from the extensive western (Eyrean) region, *substriatus* gradually occupied this vast area, which previously had been uninhabited by any member of the superspecies and, therefore, represented an empty space with an unoccupied niche. This colonization is probably a rather recent phenomenon, because no morphological differentiation has taken

place in the populations of the enormous western area, where *substriatus* has even occupied a great number of different habitats. On the other hand, *melanocephalus-uropygialis*, which has long been well established in the Torresian region, has developed no fewer than five different subspecies. To be sure, it is a sedentary tropical species, while *substriatus* has nomadic tendencies.

Finally, *striatus* invaded the continent from Tasmania and occupied the southeastern, humid parts of the country, which presented environmental conditions similar to those to which this Tasmanian bird was adapted. The contact between *striatus* and *substriatus* gave rise to the development of the hybrid population *ornatus* (which is dealt with in detail above).

The above interpretation of the history of the superspecies gives an acceptable explanation of the complicated hybridization phenomena in these birds. It appears that neighboring populations, which differ only in a few morphological characters, in all cases are able to interbreed (*uropygialis* with *melanocephalus*, *melanocephalus* with *substriatus*, and *substriatus* with *striatus*) (crosses in fig. 2). On the other hand, populations that are farther removed in space and are separated by two or more successive steps of morphological differentiation are incapable of interbreeding. Such is the case with *uropygialis* and *substriatus* in the Kimberley Division, and with *melanocephalus* and *striatus* (and *ornatus*) in southern Queensland (symbolized by a minus sign in fig. 2).

When all available facts are considered, it appears to me that the hypothesis given above is the most satisfactory one, although I admit that the problem concerning the status of *ornatus* invites further discussion. I am quite convinced that the last word has not been said on this matter.

Two other attempts have been made to describe the history of the three striated pardalotes, particularly for the purpose of explaining the origin of *ornatus*. However, neither considered the fact that *substriatus* and *melanocephalus* are very close relatives and hybridize freely.

Serventy (1953, *Emu*, vol. 53, p. 136) held *substriatus* to be of Eyrean origin, isolated west of the Great Dividing Range, whereas *striatus* was the Bassian counterpart, distributed not only in Tasmania, but also in eastern Victoria and New South Wales. These latter areas at a later date were occupied by *substriatus*, which interbred with the indigenous *striatus* and produced the hybrid population *ornatus*. It is natural to postulate an Eyrean origin of *substriatus*, when deciding the matter on the basis of the present distribution, but this interpretation faces some difficulties. How can it be explained that the populations stated to be

TABLE 1
WING MEASUREMENTS (IN MILLIMETERS) OF THE STRIATED PARDALOTES
(*Pardalotus striatus*, *Pardalotus ornatus*, AND *Pardalotus substriatus*)
(The figures in the body of the table are the number of specimens measured.
All the material is in the American Museum of Natural History.)

	62	63	64	65	66	67	68	69	70	71	Average
<i>P. striatus</i>											
Tasmania	—	—	3	1	—	1	1	1	—	1	66.5
Flinders Island	—	—	—	1	3	2	—	—	—	—	66.2
King Island	—	—	—	—	1	—	—	—	1	—	68.0
Victoria, New South Wales	—	—	—	—	2	8	1	—	—	—	66.9
<i>P. ornatus</i>											
Southeast Queensland ^a	—	—	1	—	1	—	—	—	—	—	65.0
Victoria, New South Wales	4	7	8	18	14	7	—	—	—	—	64.9
<i>P. substriatus</i>											
Southwest Queensland ^b	—	1	—	1	—	—	—	—	—	—	64.0
Victoria, New South Wales	—	2	8	5	4	1	—	—	—	—	64.7
South Australia ^c	—	1	3	4	3	3	—	—	—	—	65.1
Central Australia ^d	1	1	1	1	—	—	—	—	—	—	63.5
Southwestern Australia ^e	—	2	6	3	—	1	—	—	—	—	64.3
Kimberley Division ^f	—	2	1	—	—	—	—	—	—	—	63.3

^a Emu Vale (North Warwick), Gracemere (near Rockhampton).
^b Birdsville district.
^c Including Kangaroo Island.
^d Everard Ranges, Todmorden, Finke River.
^e North to De Grey River.
^f Mt. Alexander.

isolated east of the Great Dividing Range (*melanocephalus* in the north, *striatus* in the south) are profoundly different and unable to hybridize, while the Eyrean species (*substriatus*) is closely allied to *melanocephalus*, capable of interbreeding with it, as well as with the Bassian *striatus*, and even able to predominate in southern coastal Queensland, where the Bassian and Torresian species should be superior in the adaptation to the environment? It would be necessary to postulate that the Eyrean species was first isolated from the Torresian one, acquiring a striated head, and that the alleged Bassian *striatus* was subsequently separated from the Eyrean one. This and other discrepancies complicate matters unnecessarily, and consequently I find this hypothesis less satisfactory.

Similar objections can be raised against the theory set forth by Hindwood and Mayr (1946, Emu, vol. 46, p. 49). They advocate the view that the three striated pardalotes originally were subspecies, *sub-*

striatus inhabiting the Eyrean region, *ornatus* the continental Bassian region, and *striatus* Tasmania. The authors further explain the coexistence of all three forms as a result of range extensions in *substriatus* and *striatus*. This hypothesis poses the same difficulty as that of Serventy, as regards the relationship between *melanocephalus*, *substriatus*, and *striatus*. In addition, it implies that two neighboring species (subspecies), *substriatus* as well as *striatus*, have moved into the range of a third one (*ornatus*), which they both have occupied in its entirety but not transgressing its borders, by this procedure forming three sympatric species, but without developing the slightest differences in ecology and biology between them. This appears to be so unlikely that this hypothesis must be dismissed.

The superspecies *P. striatus* resembles *P. rubricatus* in lacking sexual dimorphism both in plumage coloration and in body proportions. It is permissible, therefore, to unite the measurements of the two sexes, as has been done in tables 1–3 of the present paper.

The members of the superspecies *P. striatus* have a very wide ecological amplitude, frequenting virtually all arboreal habitats from the humid forests to the scattered gum trees along creeks in the arid regions, but evidently they prefer the open forests of the savanna woodland areas, in which they generally are very common. After the termination of the breeding season they are more or less nomadic, at least the non-tropical populations. Off-season records must therefore not be accepted uncritically, because they may not be referable to local breeding birds but may represent stray individuals or flocks.

My study of the superspecies *P. striatus* has been based mainly on the rich material in the American Museum of Natural History, and unless stated otherwise, all statements refer to specimens belonging to this museum. In addition, the collections of the British Museum (Natural History) and the Zoological Museum, Copenhagen, have been utilized.

Pardalotus striatus (Gmelin), 1789

TYPE LOCALITY: Tasmania.

This species is commonly distributed in Tasmania and the islands of Bass Strait, and more sparingly in the southeastern continent, south and east of the Great Dividing Range, in Victoria, New South Wales, and southern Queensland, where it occasionally ranges as far north as Rockhampton. In Victoria it is found westward to about Castlemaine,¹ in New South Wales exceptionally as far west as Dubbo.

¹ There is a recent sight record from as far west as Portland (Cooper, 1961, *Emu*, vol. 61, p. 3).

Mathews (1912, *Novitates Zool.*, vol. 18 [1911], p. 387) separated the birds from King Island as *kingi*, stating that they differed from nominate *striatus* "in being uniform grey above." I have examined the type and another specimen from King Island and found them exactly similar to birds from Tasmania and from Flinders Island. Continental specimens differ slightly from Tasmanian ones in being on an average more brown on the rump and lower back and having the streaks on the crown slightly more heavy. These differences, which have been noticed also by Hindwood and Mayr (1946, *Emu*, vol. 46, p. 54), are so slight and inconstant that no subspecies can be admitted.

It appears from table 1 that the average wing length of specimens from Tasmania and from the mainland are virtually identical (66.5 and 66.9 mm., respectively). In spite of this similarity, there is a marked difference between the populations in the scattering of the measurements. Eight specimens from Tasmania have the wing length varying between 64 mm. and 71 mm., while 11 mainland birds measure 66–68 mm., the majority having a wing length of 67 mm. To be sure, both series are very small, but the difference between them may be important. I venture to advance the hypothesis that the reduced variability in the continental population may be due to gene elimination. It is a well-known fact that small populations have a trend towards genetic homogeneity, and, as already mentioned, the population of *P. striatus* on the mainland is very small compared with that of Tasmania. The scarcity of this species on the mainland is perhaps a result of competition with the closely allied *P. substriatus* and *P. ornatus*, with which it coexists, both of which are absent from Tasmania.

Pardalotus ornatus Temminck and Laugier, 1826

TYPE LOCALITY: New South Wales.

This species was formerly called *P. assimilis* Ramsay, 1878, while *ornatus* was the designation for the species that is now called *P. substriatus* Mathews, 1912. The reason for the change of name has been given by Hindwood and Mayr (*loc. cit.*).

This species, assumed to be of hybrid origin, is fully dealt with above, and it is necessary to add only a few further comments. It is restricted to the southeastern parts of Australia, east and south of the Great Dividing Range,¹ having virtually the same range and occurring in the same habitats as the continental population of *P. striatus*. It is found occasionally as far west as Portland, Onyen, Mildura, and Bourke.

¹ In Victoria also somewhat north of the Great Dividing Range.

To the north it occurs up to southeastern Queensland, locally as far north as Rockhampton. It is still a comparatively common bird north to Toowoomba-Brisbane (Lord, 1956, *Emu*, vol. 56, p. 122), but farther north it appears to be very scarce, and the few records in the northernmost part of the range may refer not to breeding birds but to accidental visitors.

In Queensland the range of *ornatus* overlaps that of *melanocephalus*, but evidently the two species do not hybridize. I have examined two specimens from Queensland in the American Museum of Natural History, and both are typical *ornatus* in color pattern as well as proportions. The first specimen was collected at Emu Vale, near Warwick, September 4, 1941, by J. R. Henry, i.e., on the same date and at the same locality, and by the same collector as the hybrid swarm *substriatus* \times *melanocephalus*, mentioned below. The other specimen is the type of *Pardalotus queenslandicus* Mathews (1923, *The birds of Australia*, vol. 11, pt. 3, p. 197), from Gracemere, near Rockhampton. Mathews gives a lengthy description of this supposedly new species but no differentiating characters, a procedure that is not now admissible according to the rules of zoological nomenclature. However, the specimen is completely similar to ones from New South Wales and Victoria.

The measurements taken of *P. ornatus* are given in table 1.

Pardalotus substriatus Mathews, 1912

TYPE LOCALITY: Victoria.

Distributed throughout the non-tropical parts of the Australian continent, including Kangaroo Island. The northern limits of the breeding range of the species are not known with certainty. It approaches the range of the tropical *P. melanocephalus uropygialis*, but there is no actual evidence of overlap.

In northwestern Australia *substriatus* has been recorded as far north as Mungi Rock Hole, 8 miles southeast of Mt. Alexander, west Kimberley. At this locality J. P. Rogers collected nine specimens, of which six were juvenile or immature birds, and he states (*in* Mathews, 1923, *The birds of Australia*, vol. 11, pt. 3, p. 206) that *substriatus* replaces *uropygialis* there. This latter is found along the Fitzroy River (Söderberg, 1918, *K. Svenska Vetenskaps. Akad. Handl.*, vol. 52, no. 17, p. 102; Shilling, 1948, *Emu*, vol. 48, p. 71), less than 50 miles to the north. I have examined the specimens from Mungi, which are in the American Museum of Natural History, and found them identical with typical *substriatus*, showing no sign of hybridization with *uropygialis*. Similarly, not a single bird in the long series of *uropygialis* from Kimberley Division, examined by me, exhibited any admixture of *substriatus*.

characters. Obviously, the two species are reproductively isolated and do not interbreed in this part of Australia.

Farther south *substriatus* commonly breeds north to the De Grey River, Pilbara Goldfield. Possibly it normally does not go much beyond this district as a breeding bird, and consequently the record from Mungi may refer to an accidental visit by a stray flock of this nomadic species. At any rate, Söderberg (*loc. cit.*) did not meet *substriatus* at Mowla Downs, which are very close to Mungi. The bird life in these barren areas is so imperfectly known that it is not possible to elucidate the matter more fully.

In Northern Territory *substriatus* breeds northward to the Macdonnell Range, but north of Alice Springs and the Finke River it is apparently very scarce, if it occurs at all. The Barclay Exploring Expedition of 1911–1912 met with neither this species nor any other pardalotes between the Macdonnell Range and latitude 16° S., apart from a single specimen obtained at 19° S. and identified as *P. ornatus* (= *substriatus*) by Hill (1913, *Emu*, vol. 12, p. 248). The wing length given (65 mm.) agrees with that of this species and certainly excludes *uropygialis*, but Campbell and Kershaw (1913, *Emu*, vol. 12, p. 277), in their comments on the material collected by the expedition, state that it is a poor specimen, kept in spirits, without label, and unidentifiable as to species. Even if the specimen belonged to *substriatus*, it is hardly probable that this record refers to a local breeding bird. More likely it represents a case of extreme nomadism.

In Queensland the northern limit runs somewhere in the southern parts of the state. A small series from Birdsville collected by Macmillan in 1940, in the American Museum of Natural History, consists of typical *substriatus*, but the species is unknown farther north in this part of the state. Specimens from Charleville are almost pure *melanocephalus* but possess a few *substriatus* characters, evidencing former hybridization. Specimens collected in the Bunya Mountains and in northern Warwick are all hybrids between *substriatus* and *melanocephalus*, not a single specimen representing the pure phenotype of *substriatus*. The hybrid zone between the two species thus extends from Charleville eastward almost to the coast. Possibly the two species do not interbreed everywhere in southeastern Queensland. Lord (*loc. cit.*) found both species breeding in the country west of Brisbane but did not notice any hybrids, whereas he found several cases of mating between *substriatus* and *ornatus*. According to Lord, *substriatus* is a common bird in this area, but to the north it rapidly decreases in number. The northernmost record is from Rockhampton.

The range of *substriatus*, as far as known, as well as the zone in which it interbreeds with nominate *melanocephalus*, is outlined in figure 1. The narrow gap between the range of *substriatus* and that of *P. melanocephalus uropygialis* in Kimberley is indicated by an arrow.

A striking parallel to the distribution pattern of these birds (*substriatus-melanocephalus-uropygialis*) is found in the superspecies *Platycercus elegans*. In South Australia *P. elegans* and *P. flaveolus* are connected by a zone of secondary intergradation, and the two subspecies that participate in the hybridization show many signs of similarity. In western New South Wales the morphological gap between the two species is much greater, and the two species are not able to hybridize but approach each other just as the two pardalotes do in Kimberley, or may even slightly overlap (Cain, 1955, *Ibis*, vol. 97, p. 460).

In its huge range *substriatus* is remarkably uniform, and it is not possible to separate any subspecies. It appears from the measurements given in table 1 that the northern birds, inhabiting hot and arid areas, have a tendency to become smaller, attaining average wing lengths that vary between 63.3 mm. and 64.0 mm., compared with 64.3 to 65.1 mm. in the populations of the more humid and cool regions. I am unable to see any geographical variation in the plumage coloration. Hindwood and Mayr (*ibid.*, p. 54) separate the birds of Western Australia as *murchisoni* Mathews, stating that they have a greater part of the crown pure black, with smaller and more drop-shaped white spots on the posterior part of the head, and the lower back and rump more brownish. I fail to see these differences. Condon (1951, *South Australian Ornith.*, vol. 20, p. 58) was likewise unable to recognize *murchisoni*.

Mathews has named a number of subspecies, which are listed below. Mathews often gave only the name of a state as a type locality, but the exact (restricted) locality, quoted from the label of the type specimen, has been added in brackets:

- substriatus*, 1912, Victoria [Ultima]
- subaffinis*, 1912, South Australia [Blackwood]
- murchisoni*, 1912, Murchison, Western Australia [Nully Pool]
- westraliensis*, 1912, Western Australia [Claremont]
- rogersi*, 1912, Mungi, interior of northwest Australia
- finki*, 1914, Finke River, Central Australia [Running Water]
- campbelli*, 1924, Kangaroo Island, South Australia

I have examined the original material, including the types, of all these forms, in the American Museum of Natural History. In the case of *campbelli*, Mathews did not choose a type, but I have examined the series on which he based the name, without, however, selecting a lecto-

type. All Mathews' names are synonyms of nominate *substriatus*. It would be a waste of paper to comment on all these alleged forms, especially as Hindwood and Mayr (*loc. cit.*) have already discussed them.

Pardalotus melanocephalus

The black-headed pardalote falls into two strikingly different groups, which are connected by a broad zone of secondary intergradation. Each has its own subspecies, and it is convenient therefore to separate them as two "subspecies groups." The remarkable parallelism between the morphological differentiation in *melanocephalus-uropygialis* and that in *punctatus-xanthopygus* has been discussed in a previous paper (Salomonson, 1961, Amer. Mus. Novitates, no. 2067, p. 14).

Melanocephalus GROUP

The upper parts are uniform grayish brown, with the rump and some of the upper tail coverts cinnamon, the flanks dull tawny brown, the supraloral spot orange, and the black loreal streak broad and conspicuous. The wing measures 60–62 mm.

Pardalotus melanocephalus melanocephalus Gould, 1838

TYPE LOCALITY: Moreton Bay, southern Queensland.

This form has its stronghold in southeastern Queensland, where it is found westward to about Charleville and northward to about Mackay. To the south it is found locally as far as Port Macquarie in north-eastern New South Wales. In the American Museum of Natural History there are only six adult specimens of this form, originating from Rockhampton, Gracemere, Charleville, and Richmond River. They have a wing length of 61–62 (average 61.7) mm. (cf. table 3). The very slight scattering of these measurements is probably due to insufficient material. A single specimen from "Queensland" in the Zoological Museum, Copenhagen, has a wing length of 62.5 mm.

The discovery of an extensive hybrid zone between *substriatus* and nominate *melanocephalus* was a surprise to me, because the existence of such a zone was quite unexpected. Nobody has suspected that these two species interbreed, and there are no published statements of hybridization, nor even comments on the possibility. It is worth mentioning, however, that some specimens collected on Stradbroke Island, southern Queensland, differ from typical *melanocephalus* in having "lores rather different from type, *i.e.* smaller and not so marked in hue" (Mathews, 1924, The birds of Australia, vol. 11, pt. 4, p. 214). This difference may be due to interbreeding with *substriatus*, because the more narrow and

indistinct loral streak is a *substriatus* character.

The hybrid zone extends from Charleville southeastward through southern Queensland, probably right to the coast. The center of the zone appears to be in northern Warwick. J. R. Henry collected five adult specimens there (at Emu Vale) in 1941, and all of them show a strong mixture of *substriatus* and *melanocephalus* characters. Of four specimens from Bunya Mountains collected near Dalby in 1940 by J. R. Henry (one by L. Macmillan), one is a typical *melanocephalus*, and three

TABLE 2
CHARACTERS OF THE HYBRIDS BETWEEN *Pardalotus substriatus*
AND *Pardalotus melanocephalus*

(Symbols: s, *substriatus*; m, *melanocephalus*; i, intermediate between the two species.)

No.	Locality	Sex	I ^a	II	III	IV	V	(Wing length) ^b	No. of Characters		
									s	i	m
1	Charleville	♂	m	i	m	m	m	(62) ^b	0	1	4
2 ^c	Bunya Mountains	♂	m	m	m	m	m	(62)	0	0	5
3 ^c	Bunya Mountains	♂	i ^d	s	s	i	s	(64)	3	2	0
4	Bunya Mountains	♀	i ^d	i ^e	i	m	m	(60)	0	3	2
5	Bunya Mountains	♀	i ^d	i ^d	m	m	m	(62)	0	2	3
6 ^c	North Warwick	♀	i	i	s	m	s	(64)	2	2	1
7 ^c	North Warwick	♂	i	i ^e	i	s	m	(61)	1	3	1
8 ^c	North Warwick	♂	i	s	s	i	m	(62)	2	2	1
9 ^c	North Warwick	♂	s	s	m	m	m	(60)	2	0	3
10	North Warwick	♀	s	s	m	s	s	(63)	4	0	1

^a For symbols I-V, see text (pp. 22-23).

^b Figures in parentheses are the wing lengths in millimeters.

^c Illustrated in figure 3.

^d Nearest to *melanocephalus*.

^e Nearest to *substriatus*.

are hybrids, but with a phenotype approaching that of *melanocephalus*, as is a single adult specimen from Charleville collected by Macmillan in 1940.

It is necessary briefly to enumerate the morphological differences between the two parental species in order to give a description of the hybrids. The presence or absence of striation on the head is, of course, the most conspicuous difference, but there are other noteworthy differences. *Pardalotus substriatus* and *P. melanocephalus* (n nominate form) differ in the following points:

I. CROWN: In *P. substriatus*, striated; in *P. melanocephalus*, uniform black.

II. SIDES OF FACE: *Pardalotus substriatus* with suborbital area, ear coverts, and

sides of nape white, usually with blackish feather edges which give a speckled and streaked appearance but which do not produce a marked contrast to the whitish sides of throat; loreal streak rather narrow, usually black, but in some individuals mixed with white. *Pardalotus melanocephalus* with a broad, uniform, black band covering lores, suborbital region, ear coverts, and sides of nape, strongly contrasting with the white sides of throat.

III. SUPRALORAL PATCH: In *P. substriatus*, yellow; in *P. melanocephalus*, orange.

IV. RUMP: In *P. substriatus*, tawny brown; in *P. melanocephalus*, warmer brown, nearest cinnamon.

V. WING LENGTH: In *P. substriatus*, 63–67 mm.; in *P. melanocephalus*, 61–62 mm.

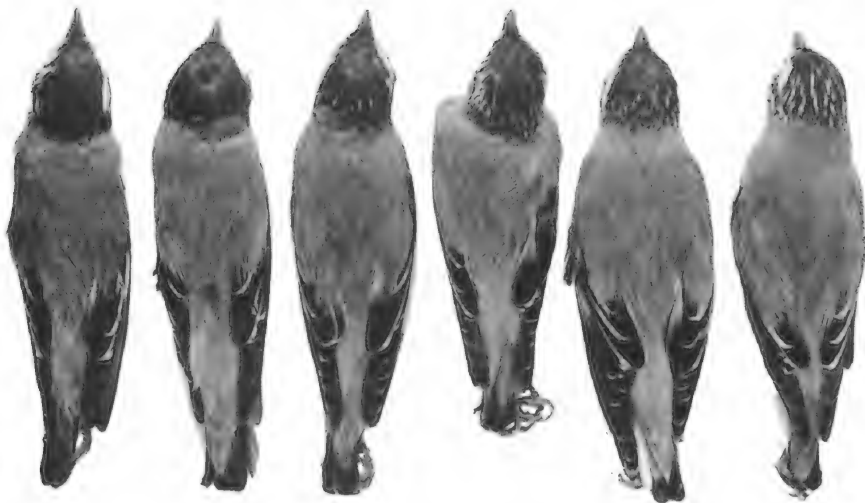


FIG. 3. Hybrids between *Pardalotus melanocephalus* and *P. substriatus*, showing (from left to right) increasing striation on the head. The specimens are (also from left to right) those that are designated, respectively, as numbers 2, 3, 6, 7, 8, and 9 in table 2. Photograph by the American Museum of Natural History.

The combination of these five characters in the individuals of the hybrid populations is shown in table 2. Only one of these specimens is a typical *melanocephalus* (specimen 2 in table 2). There is not a single typical *substriatus*, although specimen 10 comes very near, possessing only the orange supraloral streak of *melanocephalus* and being similar to *substriatus* in all other particulars. It appears from table 2 that the five characters (I–V) in which the two species differ vary independently of one another, characters belonging to one species being freely combined with those belonging to the other species. Six of the hybrid specimens enumerated in table 2 are shown in figure 3, arranged in a series

showing increasing striation on the head, from the pure *melanocephalus* type to the pure *substriatus* type. Two specimens are particularly interesting, namely, numbers 3 and 9 (both shown in fig. 3). Number 3 superficially resembles *melanocephalus*, with an almost pure black crown and with only fine striations on the nape, but the sides of the face and the supraloral patch are the color of those of *substriatus*, and even the proportions are those of *substriatus*. Number 9, on the contrary, resembles a typical *substriatus*, with a striated crown, but the color of the supraloral patch and of the rump, and the proportions, are those of *melanocephalus*. These two examples suffice to demonstrate the thorough mixing of the parental characters in the hybrids.

Some uncertainty attaches to the evaluation of the wing length as a specific character. In table 2 measurements of 63–64 mm. have been interpreted as a *substriatus* character, because *melanocephalus* does not exceed 62.5 mm. in wing length. As the material of pure *melanocephalus* (of the nominate subspecies) is very small, it is impossible to assert that specimens belonging to the nominate form may not attain greater wing lengths. On the other hand, no fewer than 55 specimens of *substriatus* have been measured (cf. table 1), and of these only one, from central Australia, had a wing length as small as 62 mm. A total of 22 specimens from Queensland, New South Wales, and Victoria measured 63–67 mm. It is safe, therefore, to conclude that a wing measurement of only 60–62 mm. is a *melanocephalus* character.

It is noteworthy that, in spite of all the differences between *melanocephalus* and *substriatus*, the wing pattern is exactly similar in the two species. In this respect all hybrids examined are identical with the two parental species, which tends to show that neither *ornatus* nor *striatus* has participated in the hybridization. The capture of a pure *ornatus* in the center of the hybrid zone (mentioned above, p. 18) strengthens this view. Undoubtedly, the wing pattern in *melanocephalus* is important as a species recognition and discriminating mark, which prevents interbreeding with *ornatus* and *striatus* but not with *substriatus*. In this last species, the wing pattern does not serve the function of species recognition, or at any rate has a reduced threshold in this respect, or *substriatus* would not be able to interbreed with *ornatus* in southern Queensland.

***Pardalotus melanocephalus bowensis*, new subspecies**

TYPE: A.M.N.H. No. 699100; Bowen, central eastern Queensland; originally from the Museum Godeffroy.

Similar to nominate *melanocephalus* but differing in having deeper cinnamon, or even chestnut, rump and more cinnamon on the scapulars

and flanks, and in being slightly smaller. The wing length in four specimens is 60–62 (average, 61.0) mm. (table 3).

This subspecies is restricted to the central part of eastern Queensland, from about Mackay north to Cardwell. Four specimens, from Bowen, Inkerman, and Cardwell, have been examined in the American Museum of Natural History.

Pardalotus melanocephalus barroni Mathews, 1912

TYPE LOCALITY: Cairns.

This subspecies forms an assemblage of heterogeneous units and constitutes the hybrid population between *bowensis* and *uropygialis* already mentioned. Because the hybrid zone is of considerable extent, I find it practical to give the hybrid population a special designation, and a name (*barroni* Mathews) is already available. Another reason for separating the hybrid population nomenclatorially is the fact that it would be misleading to unite it with *bowensis* or *uropygialis*, because only exceptional individuals inhabiting the hybrid zone have the phenotype of the parental forms, the great majority being intergrades of a very different appearance.

The hybrid zone is rather sharply delimited. It stretches across northern Queensland, from Cairns and Cooktown to Normanton, and in reaching the Gulf of Carpentaria cuts off the pure *uropygialis* population of Cape York Peninsula from the main population of this form (see fig. 1). The hybrid zone appears, roughly speaking, to coincide with the subhumid region in northern tropical Queensland, both the semi-arid region south of it (Cloncurry) and the humid region north of it (Cape York) being inhabited by pure *uropygialis*. The restriction of the hybrid zone to the subhumid environment indicates that the hybrids have a reduced survival value outside it, while, on the other hand, the virtual absence of the two parental forms within the hybrid zone tends to show that the hybrids have a considerable selective advantage in that area, which would account for the sharp delimitation of the hybrid zone.

The hybrid population is characterized by its enormous variation, both individually, in the composition of the single population, and geographically, in the continuous change from one locality to the other.

The intrusion of *uropygialis* genes alters the phenotype of *bowensis* as follows: The deep cinnamon rump becomes more or less suffused with golden yellow, this being the most conspicuous character. Further, the supraloral patch becomes brighter orange, the loreal and suborbital region white, and the upper parts become slightly paler. This last character is not always easy to see, particularly in birds with worn and

TABLE 3
WING MEASUREMENTS (IN MILLIMETERS) OF *Pardalotus melanocephalus*
(The figures in the body of the table are the number of
specimens measured. All the material belongs to the American Museum
of Natural History.)

	56	57	58	59	60	61	62	63	Average
<i>melanocephalus</i>									
Southern Queensland	—	—	—	—	—	2	4	—	61.7
<i>bowensis</i>									
Central eastern Queensland	—	—	—	—	1	2	1	—	61.0
<i>barroni</i>									
Cairns	—	2	1	—	3	2	—	—	59.3
Cooktown	—	—	—	1	—	—	—	—	
Normanton	1	1	2	1	3	—	—	—	58.3
<i>uropygialis</i>									
Sedan (Cloncurry)	—	—	—	—	1	1	—	—	60.5
Northern Territory ^a	—	—	1	1	1	—	—	—	59.0
Napier Broome Bay ^b	—	—	1	3	1	1	1	1	60.1
Forrest River ^b	—	1	—	1	—	—	—	—	58.0
Marngle Creek ^b	—	—	1	1	—	—	—	—	58.5
Parry's Creek ^b	2	—	2	1	1	—	—	—	57.8
Derby, Point Torment ^b	1	3	1	3	2	—	—	—	58.2
<i>melwillensis</i>									
Melville Island	2	5	4	2	1	—	—	—	57.7
<i>restrictus</i>									
Cape York Peninsula ^c	1	2	—	1	—	—	—	—	57.3

^a Arnhem Land, South Alligator River.

^b Situated in Kimberley Division, northwestern Australia.

^c Jardine River, Cape York.

abraded plumage. Finally, the proportions become smaller. This alteration appears in the following measurements of wing lengths: in pure *boweni*, 60–62 (average, 61.0) mm.; in *barroni* from Cairns (nearest to *bowensis*), 57–61 (average, 59.3) mm.; in *barroni* from Normanton (nearest to *uropygialis*), 56–60 (average, 58.5) mm.; and in pure *uropygialis* from northwest Australia, usually 56–60 mm., with averages of 57.8–58.2 mm. The individual measurements of the hybrids are given in table 3.

I have examined the following specimens of the hybrid population:

CAIRNS: Eight specimens, including the type of *barroni* from Barron River. Specimens 1–6 are fairly similar and show a perfect blending of

uropygialis and *bowensis* characters. They differ from *bowensis* in having the rump chestnut, with a strong golden tinge, the scapulars with a stronger cinnamon tinge, the supraloral patch distinctly deeper orange, the flanks uniform cinnamon, and the proportions slightly smaller. The type specimen of *barroni* belongs to this series. Specimen 7 approaches *bowensis* but has brighter cinnamon on rump and flanks and no golden tinge on the rump. Specimen 8 has a yellow rump like that of *uropygialis* and differs from this form only in having the broad black loreal streak and the comparatively dark upper parts of *bowensis*.

COOKTOWN: One specimen, which is near typical *uropygialis* but has slightly darker upper parts and a conspicuous cinnamon tinge on the lower back and on the yellow rump.

NORMANTON: This locality, near the Gulf of Carpentaria, is situated close to the western boundary of the hybrid zone, and the population differs in its composition considerably from that inhabiting Cairns, and approaches *uropygialis* in appearance. Ten specimens have been examined. Specimen 1 is intermediate between *bowensis* and the type specimen of *barroni*, described above. Specimens 2–5 are very similar to the type specimen of *barroni*. Specimens 6–9 approach strongly typical *uropygialis*, having only a faint cinnamon tinge on the yellow rump and resembling the specimen from Cooktown, although slightly brighter yellow on the rump than this specimen. Specimen 10 is virtually indistinguishable from *uropygialis*. The birds from Normanton are generally slightly paler on the upper parts than those from Cairns and Cooktown and have, further, usually more white on the lores, both these characters representing approaches to *uropygialis*.

Uropygialis GROUP

The upper parts are paler gray than in the *melanocephalus* group, and the rump and some of the upper tail coverts are bright cadmium yellow, the scapulars paler than in *melanocephalus* (isabelline-colored or pale sandy brown), the flanks, similarly, brighter cinnamon or sandy brown, not so dull tawny brown, the supraloral spot deeper and brighter orange, and the facial color pattern supplied with more white, the sides of nape, the ear coverts, the suborbital region and the lores being white, only a thin black line remaining on the lores, edging the orange supraloral patches ventrally. The proportions are smaller than those of *melanocephalus*, the wing length being generally 56–60 mm.

Pardalotus melanocephalus uropygialis Gould, 1840

TYPE LOCALITY: Port Essington, Northern Territory.

This form inhabits northern Australia (range outlined in fig. 1) but does not penetrate southward into the arid zone. It appears to be very uniform in its extensive range from east to west, as far as the semi-arid and subhumid zones are concerned. Two specimens from Cloncurry, northwest Queensland, virtually do not differ from birds inhabiting the distant Kimberley Division of northwestern Australia. The birds of the humid parts of Northern Territory, from whence I have examined three specimens from the South Alligator River, not far from the type locality of *uropygialis*, are slightly darker on the upper parts and have a slightly more orange rump, but this difference indicates just a slight approach to the dark form of adjacent Melville Island and does not justify the separation of further subspecies.

Mathews separated the birds from Cloncurry River as *sedani* but compared them only with the very different hybrid population (*barroni*) of Cairns. I have examined the type and a cotype; both are indistinguishable from northwest Australian *uropygialis*. Mathews separated the birds from the coast of western Kimberley as *tormenti*, stating that they were paler than topotypical *uropygialis*. I have seen the type and a good series from the type locality, and, as mentioned, they are not quite so dark as specimens from the South Alligator River, but the difference is slight and not constant. Mathews also described the birds from Parry's Creek, in the interior of Kimberley, as *inexpectatus*, which were said to differ from *uropygialis* in being darker. The type is a not fully adult specimen, but neither this nor the other specimens from the type locality differ from the large series of birds from other localities in Kimberley.

Compared with nominate *melanocephalus* and *bowensis*, *uropygialis* has distinctly smaller proportions. The wing length of the specimens examined is given in table 3. It appears that in most populations it varies between 56 mm. and 60 mm., with averages of 57.8–59.0 mm. It is strange, however, that the population of Napier Broome Bay, on the north coast of northwest Australia, differs remarkably in measurements, attaining a larger size than all the other populations of *uropygialis*. The wing of eight adult specimens measures 58–63 (average 60.1) mm.

Pardalotus m. uropygialis apparently does not range south of the Fitzroy River in Kimberley. J. P. Rogers collected a good series at various localities not far from that river (Parry's Creek, Marngle Creek), but not farther south. At Mungi Rock Hole, 8 miles southeast of Mt. Alexander, he met *P. substriatus* and collected a series (cf. p. 18), which tends to show that the two species behave as two allopatric species in this part of Australia, as *P. punctatus* and *P. xanthopygus* do farther south in Western Australia.

There is, however, a somewhat dubious sight record of *uropygialis* in the Pilbara District made by F. L. Whitlock in 1909. It would be of great interest if *uropygialis* occurs there, because it would imply that it actually overlaps *substriatus*. Unfortunately, no specimens of *uropygialis* have ever been collected there, and Serventy and Whittell (1951, A handbook of the birds of Western Australia, p. 311), discussing Whitlock's record, exclude *uropygialis* from this region. Even Mathews (1924, The birds of Australia, vol. 11, pt. 4, p. 214) regrets that Whitlock did not collect any specimens in Pilbara, but three pages later (p. 217) he mentions his own form, *Pardalotinus melanocephalus pilbarra*, described the previous year from Pilbara Goldfield. Because no type or other specimens from this area are present in the Mathews collection in the American Museum of Natural History, and because specimens from the Pilbara region are altogether unknown, Mathews obviously made some mistake in describing this form, and I think that we safely can ignore it.¹

It is noteworthy that *P. substriatus* freely hybridizes with nominate *melanocephalus* in eastern Australia, while it is reproductively isolated from *uropygialis* in western Australia. The morphological differences between *uropygialis* and *substriatus* are much greater, however, than those between nominate *melanocephalus* and *substriatus*, this being so of the facial pattern, particularly the color of the supraloral patch, the proportions, and, above all, the color of the rump.

Pardalotus melanocephalus melvillensis Mathews, 1912

TYPE LOCALITY: Melville Island, Northern Territory.

Differs strikingly from *uropygialis* in having the rump deep orange, not yellow, the supraloral patch vermilion, not orange, the upper parts darker, of the same shade as in nominate *melanocephalus* and *bowensis*, the flanks much darker cinnamon, and the under parts slightly deeper and brighter yellow. The proportions are similar to those of *uropygialis*, the wing length of 14 adult specimens being 56–60 (average, 57.7) mm.

This form inhabits Melville Island. A long series, including the type, was examined in the American Museum of Natural History.

Pardalotus melanocephalus restrictus, new subspecies

TYPE: A.M.N.H. No. 699113; adult male; Jardine River, Cape

¹Amadon (1951, Amer. Mus. Novitates, no. 1504, p. 9) mentions a similar example of Mathews' extremely careless way of describing new subspecies, believing that he "merely proposed the new name in the hope that it might later prove valid."

York; April 16, 1911; collected by McLennan.

Very similar to *melvillensis* and agreeing with this form in having darker upper parts than *uropygialis*, deep orange rump and brighter yellow under parts, but differing in having the flanks paler and the supra-loral patch orange, as in *uropygialis*. The proportions apparently do not differ from those of *melvillensis*; the wing length of four specimens is 56–59 (average, 57.3) mm.

This form is restricted to the northern parts of Cape York Peninsula. I have seen only four specimens (Jardine River, two; Cape York, two), two of which have worn plumage. This subspecies differs only slightly from *melvillensis*. It illustrates the phenomenon, known in a number of other birds, that the populations of Melville Island and Cape York, inhabiting areas with a very similar humid regime, have developed in a parallel way, attaining darker and more saturated plumage colors than the populations of the adjacent subhumid and semi-arid zones.

TYPE SPECIMENS EXAMINED

Pardalotus striatus kingi Mathews, 1912 = *P. striatus*. In the American Museum of Natural History.

Pardalotus striatus substriatus Mathews, 1912 = *P. substriatus*. In the American Museum of Natural History.

Pardalotus striatus subaffinis Mathews, 1912 = *P. substriatus*. In the American Museum of Natural History.

Pardalotus striatus murchisoni Mathews, 1912 = *P. substriatus*. In the American Museum of Natural History.

Pardalotus striatus westraliensis Mathews, 1912 = *P. substriatus*. In the American Museum of Natural History.

Pardalotus striatus rogersi Mathews, 1912 = *P. substriatus*. In the American Museum of Natural History.

Pardalotus striatus finki Mathews, 1914 = *P. substriatus*. In the American Museum of Natural History.

Pardalotus striatus campbelli Mathews, 1924 = *P. substriatus*. In the American Museum of Natural History. No type specimen was selected by the describer, but I have examined all the material on which Mathews based the description.

Pardalotus queenslandicus Mathews, 1923 = *P. ornatus*. In the American Museum of Natural History.

Pardalotus melanocephalus bowensis Salomonsen, 1961 = *P. m. bowensis*. In the American Museum of Natural History.

Pardalotus melanocephalus barroni Mathews, 1912 = *P. m. barroni*. In the American Museum of Natural History.

Pardalotus melanocephalus inexpectatus Mathews, 1912 = *P. m. uropygialis*. In the American Museum of Natural History.

Pardalotus melanocephalus tormenti Mathews, 1912 = *P. m. uropygialis*. In the American Museum of Natural History.

Pardalotus melanocephalus sedani Mathews, 1913 = *P. m. uropygialis*. In the American Museum of Natural History.

Pardalotus melanocephalus melvillensis Mathews, 1912 = *P. m. melvillensis*. In the American Museum of Natural History.

Pardalotus melanocephalus restrictus Salomonsen, 1961 = *P. m. restrictus*. In the American Museum of Natural History.

ERRATUM

In "Notes on flowerpeckers (Aves, Dicaeidae). 2. The primitive species of the genus *Dicaeum*" (1960, Amer. Mus. Novitates, no. 1991), line 3 from the top on page 11 should read: "much darker and heavier streaks on the under parts. The extension," not "... upper parts."

ADDENDUM

Deignan (1960, November 1, Bull. Brit. Ornith. Club, vol. 80, no. 8, p. 143) has questioned the validity of the selection of the lectotype of *Prionochilus modestus* Hume, 1875 (= *Dicaeum agile modestum*), published by me (Salomonsen, 1960, March 1, Amer. Mus. Novitates, no. 1991, p. 9). Because Hume did not choose a type specimen, a lectotype was chosen by the British Museum authorities (probably Sharpe) from the specimens belonging to Hume's original series, but this was not published. I mentioned this lectotype in the following sentence: "The type specimen of *modestum*, which I have examined in the British Museum, was collected at Mergui by W. Davison and is a fine, fresh-molted, adult male." The publication of this statement made the selection of the lectotype effective, even if I did not give further particulars. The selection became valid, because (1) I referred to a definite specimen, (2) this specimen is marked as the type, (3) the specimen is found in the collection of a named public museum, and (4) I myself expressly stated that I considered this specimen the type. The lectotype, so selected, constitutes the only valid basis for the name *modestum*, and all restrictions of the type locality are irrelevant from a nomenclatorial point of view. But even if this were not the case, my restriction to Mergui, expressly stated in my paper (p. 8) antedates all subsequent restrictions. For this reason alone Deignan's selection of Maliwun as the restricted locality is untenable.

There are also some practical reasons that make it incorrect to change my arrangement of the two components of Hume's composite species *modestum*, performed by me in my capacity of first reviser, but I find it unnecessary to go into further details.

